CONVERGENT VESSEL DIAMETER–STEM DIAMETER SCALING ACROSS FIVE CLADES OF NEW AND OLD WORLD EUDICOTS FROM DESERT TO RAIN FOREST

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Premise of research.   Variation in average xylem vessel diameter across species has important functional consequences, but the causes of this variation remain unclear. Average vessel diameter is known to scale with stem size within and across species. Vessel diameter also seems to differ between clades and across environments, with dryland plants having narrower, more cavitation-resistant vessels. As a result, it is not clear to what extent phylogenetic affinity and environment are associated with differences in the vessel diameter–stem size relationship.

Methodology.   With linear models and correlations, we explored the influence of environment and phylogeny on the vessel diameter–stem diameter relationship in a molecular phylogenetic context across 83 species in four families spanning desert to rain forest in the Americas, Africa, Asia, and Madagascar.

Pivotal results.   Mean species vessel diameter was strongly predicted by trunk diameter (slope ~0.33), and this slope was not affected by either phylogenetic affinity or environment. Clades differed only slightly in mean vessel diameter when controlling for stem size, and there was no tendency for plants of moist environments to have wider vessels. Of four climate indexes, only the temperature index contributed to explaining vessel diameter, although very weakly.

Conclusions.   Our results are congruent with models suggesting that natural selection should maximize vessel conductivity while minimizing cavitation risk via vessel taper in the context of conductive path length. Because neither environment nor phylogeny contributed to explaining vessel diameter–stem diameter scaling across species, our results appear congruent with the notion that selection favoring cavitation resistance via narrow vessels should lead to shorter statures independently of ancestry or habitat. The repeated finding of narrow vessels in dryland plants might therefore reflect the smaller average stem size of plants in drylands rather than the plants having vessels that are narrow for their stem diameters.

Keywords: allometry, comparative methods, conduit taper, ecological wood anatomy, linear mixed models, xylem vessels.

Online enhancement: appendix.

Introduction

Across species, organismal size predicts myriad attributes ranging from metabolic rate to organ proportionalities (Schmidt-Nielsen 1975; West et al. 1997). Circulatory systems are no exception, and across wide phylogenetic spans, body size often predicts features such as orders of branching, length, and diameters of conduits (Holt et al. 1981). In woody plants, the circulatory system that conducts water from roots to leaves

is made up of vessels or tracheids. Just as whales have wider aortas than mice do, larger plants have long been known to have wider conduits at their bases than small plants do (Grew 1682; Sanio 1872; de Bary 1884). Recent studies of the relationship between conduit dimensions and stem size have shown that vessel diameter scales predictably with stem length or diameter (Anfodillo et al. 2006). The relationship seems to be a general one and has been recovered both within species and over species mean values drawn from across the woody plant phylogeny (Olson and Rosell 2006, 2013; Petit et al. 2008, 2010). With its apparent pervasiveness, this pattern demands explanation. Complicating any such explanation are observations that average conduit diameter across species

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seems to be predicted by factors such as climate and phylogenetic affinity and not just stem size. It is therefore still unclear to what extent the putatively pervasive conduit diameter–stem size relationship can in fact be altered across habitats and clades. Here we briefly review reasons for expecting vessel-stem scaling to vary with environment and phylogeny before turning to our sampling and testing procedure.

There are centuries' worth of literature documenting wider conduits in larger stems (recent examples include Carlquist 1966, 1969, 1984, and many others; Aloni and Zimmermann 1983; Rury 1985; Baas et al. 1988; Ewers et al. 1990; Butterfield et al. 1993; Lens et al. 2004; Olson and Rosell 2006; Wheeler et al. 2007; Christensen-Dalsgaard et al. 2008; Terrazas et al. 2008; Zach et al. 2010; Vázquez-Sánchez and Terrazas 2011). However, the notion that stem size should predict average vessel dimensions seems contradicted by the reiterated observation that average vessel diameter appears to reflect climate. By far the most frequently corroborated result of studies that document wood anatomical variation across habitats is that plants in drier areas have narrower vessels than plants in moist areas (Carlquist 1966, 1975, 1980, 1984, 1985, 2001; Baas et al. 1983; Baas and Carlquist 1985; Barajas-Morales 1985; Carlquist and Hoekman 1985; Lindorf 1994; Segala-Alves and Angyalossy-Alfonso 2000; Lens et al. 2004; Fisher et al. 2007; Bosio et al. 2010; etc.). Differences in mean vessel diameter between individuals of similar growth form across environments are attributed to the relative conductive safety and efficiency of narrow vessels versus wide vessels. Narrow vessels are regarded as resisting cavitation better and so would be favored in drier areas, whereas wetter conditions put plants at less cavitation risk and so favor wider, more conductively efficient vessels (see also Tyree and Sperry 1989; Tyree et al. 1994; McCulloh and Sperry 2005; Hacke et al. 2006; Sperry et al. 2008; Cai and Tyree 2010). This explanation seems to counter the idea that average vessel diameter should be determined by stem size, because if vessel diameter is predicted by stem size, then the vessels of a rain forest plant would be of similar average diameter to those of a desert plant of similar stem dimensions. Our goal here is to explore the seeming pervasiveness of the vessel diameter–stem size relationship, so we ask how environmental variation might affect this relationship. Specifically, we ask whether climate variables that seem likely associated with water availability and cavitation risk can help predict mean conduit diameter or variation in the vessel diameter–stem size relationship. This approach allows us to address the traditional expectation that vessel diameter in areas of high water availability and low cavitation risk should be wider for a given stem size than in plants growing in areas of low water availability and presumably high cavitation risk (Carlquist 1989).

Vessel diameter has also been found to vary between clades, and this factor also seems to be a possible influence on the vessel diameter–stem size relationship. Previous studies of vessel scaling have sampled either intensively within species or broadly across the woody plants (Anfodillo et al. 2006; Weitz et al. 2006; Coomes et al. 2007; Mencuccini et al. 2007; Nygren and Pallardy 2008; Sperry et al. 2008; Terrazas et al. 2008; Fan et al. 2009; Petit et al. 2010; Petit and Anfodillo 2011; Olson and Rosell 2013). Particular vessel diameters or ranges of diameters are often cited as potentially diagnostic of

species or clades (IAWA 1989; Herendeen and Miller 2000; Lens et al. 2005, 2009; Basconsuelo et al. 2011). Moreover, many quantitative features in organisms are often more similar among closely related species than distantly related ones, a pattern often referred to as phylogenetic signal or "inertia" (Hansen and Martins 1996; Blomberg et al. 2003; Revell 2010). It therefore seems possible that variation in vessel diameter across clades could reflect common ancestry even as stem size varies, revealing differences in the vessel diameter–stem size relationship.

Despite reasons to expect the vessel-stem relationship to vary between environments or clades, no study to date has simultaneously spanned wide phylogenetic and environmental ranges with intensive sampling within clades. Wide ranges in climate, stem size, and habit, both within and across clades, are important for such studies because they should maximize the chance of observing any phylogenetic or environmentally associated deviations in vessel diameter–stem size relations. To attain appropriately wide ranges, we documented variation in vessel and stem diameters in 83 species across North America, South America, Africa, Asia, and Madagascar. The species spanned warm, hyperwet tropical lowland and highland habitats to frost-prone deserts and ranged from deciduous to evergreen trees and shrubs, including seven stem succulents (fig. 1). Our sampling ranged from species with marked growth rings in highly seasonal locales to those with no detectable rings growing in climates with very little fluctuation in temperature and rainfall throughout the year. By sampling across a very wide range of life-forms, wood anatomical modes, and habitats, we substantially increased the likelihood of finding departures from any vessel diameter–stem diameter scaling. Studying distant phylogenetic relations tests the extent of convergence between the descendants of distant ancestors, whereas close relatives show the degree to which divergence (or lack of phylogenetic "inertia") is possible across the descendants of the same common ancestor. We included both close and distant relations by studying representatives of five clades of eudicots, *Bursera* and *Commiphora* of Burseraceae (Sapindales, Rosids II in Angiosperm Phylogeny Group 2009), *Moringa* (Moringaceae, Brassicales, Rosids II), the *Pedilanthus* clade of *Euphorbia* (Euphorbiaceae, Malpighiales, Rosids I), and Gentianaceae tribe Helieae (Gentianales, Asterids). This combination of clades represents an ideal situation in which to challenge the notion of widespread or "universal" scaling between vessel diameter and stem dimensions irrespective of clade and environment (Lundgren 2004; Anfodillo et al. 2006; Coomes et al. 2007). Finding that vessel diameter scales with stem diameter in similar ways across these clades and environments would add support to hypotheses that attempt to explain vessel taper as a function of stem size (Anfodillo et al. 2006; Mencuccini et al. 2007; Savage et al. 2010). Finding that the vessel diameter–stem diameter relationship differs between clades or environments would show that the vessel diameter–stem size relationship is not as widespread or "universal" as thought. Either result would require explanation and indicate directions for further work. In this vein, we discuss our results in the light of recent hydraulic scaling models and the relationship between vessel diameter, conductive path length, and stem diameter.
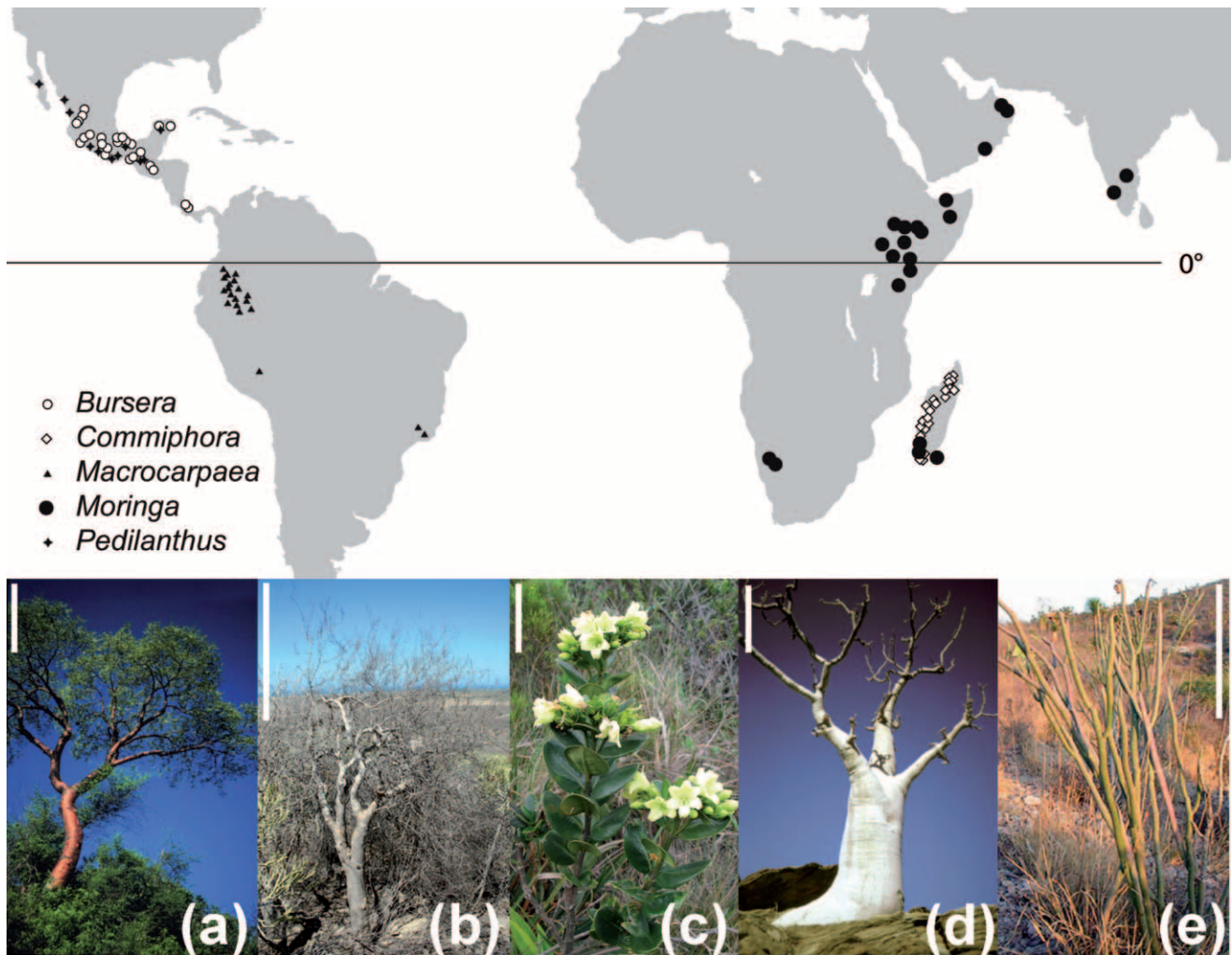
Fig. 1 Morphological, environmental, and geographical diversity in sampling. Geographic and environmental sampling covers desert, tropical rain forest, cloud forest, tropical dry forest, and other habitats across North America, South America, Africa, Asia, and Madagascar. *a*, *Bursera longipes* (Burseraceae), a tree of Mexican tropical dry forest. *b*, Malagasy *Commiphora mahafaliensis* (Burseraceae) in scrub overlooking the Mozambique Channel. *c*, *Macrocarpaea subsessilis* (Gentianaceae) shrub in an Ecuadorian cloud forest. *d*, *Moringa ovalifolia* (Moringaceae) of the Namib Desert. *e*, Mexican tropical dryland *Euphorbia tehuacana* (Euphorbiaceae), a stem succulent. Scale bars = 1 m in *a*, *b*, and *e*; 5 cm in *c*; and 20 cm in *d*.

Methods

Sampling and Anatomical Measurements

We generated original anatomical data for three clades and drew vessel- and stem-diameter data from our published studies of two additional clades (tables 1, B1; tables B1–B4 available online; app. A). We sampled 15 species of tree and shrub *Bursera* from rain forest to seasonally dry tropical forest in Mexico and Central America (Burseraceae, Sapindales, Rosids II; fig. 1*A*). Our sampling includes most species of the *simaruba* clade plus relatives from other clades within subgenus *Bursera*, of which the *simaruba* clade is a member. We collected 22 species of *Commiphora* and two samples of *Ambilobea*, also burseraceous trees and shrubs, from an array of seasonally dry tropical habitats across Madagascar (fig. 1*B*). Our sampling

includes most species of the two Malagasy clades of *Commiphora* (Weeks and Simpson 2007). We also collected samples from 14 of the 15 species of the *Pedilanthus* clade of *Euphorbia* (Euphorbiaceae, Malpighiales, Rosids II; Cacho et al. 2010), spanning desert to cloud forest in Mexico and including habits such as stem succulents, evergreen shrubs, and deciduous trees (fig. 1*C*). Carlquist and Grant (2005) provided data on stem and vessel diameter from 19 species of the gentianaceous tribe Helieae, mostly of the genus *Macrocarpaea* but with some samples of *Symbolanthus* and *Tachia* (Gentianales, Asterids I). These species are evergreen shrubs and trees of low- to highland wet tropical vegetation largely from the Andes in northwestern South America (fig. 1*D*). *Macrocarpaea* has more than 100 species, whereas *Symbolanthus* has ~30 and *Tachia* has ~10. Olson and Carlquist (2001) and Olson and Rosell (2006)

Table 1

Sample Sizes and Morphological and Environmental Ranges of the Clades Studied

Clade: order, family, genera	No. species	No. samples	SD (cm)	VD (μm)	MAT (°C)	MAP (mm)	Habitats	Habits
Bursera: Sapindales, Burseraceae, *Bursera*	15	64	9.9–60.81 (32.6)	70.8–109.9 (88.5)	20.3–28.2 (25.1)	661.7–1446.8 (952.8)	Tropical rain to dry forest	Deciduous shrubs to evergreen trees
Commiphora: Sapindales, Burseraceae, *Commiphora*, *Ambilobea*	22	79	2.0–32.0 (12.2)	55.6–108.5 (79.0)	23.9–26.8 (24.8)	376.0–1222.0 (692.5)	Moist to dry tropical deciduous forest	Deciduous shrubs to trees
Macrocarpaea: Gentianales, Gentianaceae, *Macrocarpaea*, *Symbolanthus*, *Tachia*	19	20	.7–6.1 (2.7)	27.0–57.0 (41.6)	9.1–25.2 (16.7)	392.0–2981.0 (1399.5)	Lowland to highland tropical wet forests	Evergreen shrubs and treelets
Moringa: Brassicales, Moringaceae, *Moringa*	13	21	6.9–116.9 (88.5)	56.7–191.4 (128.7)	19.3–28.7 (25.5)	97.0–1100.8 (496.1)	Desert to tropical dry forest	Deciduous water-storing trees to tuberous shrub(let)s
Pedilanthus: Malpighiales, Euphorbiaceae, *Pedilanthus* clade of *Euphorbia*	14	39	.9–12.6 (3.1)	25.2–80.9 (34.07)	17.5–25.5 (21.7)	146.0–3619.0 (1192.6)	Temperate desert, tropical dry forest to tropical cloud forest	Leafless stem succulents, evergreen shrubs, deciduous trees

Note. Clade name is the code name used in all tables and figures. Order from Angiosperm Phylogeny Group (2009). SD, per-species average stem diameter; clade means in parentheses. VD, vessel diameter. MAT, mean annual temperature. MAP, mean annual precipitation.

provided vessel- and stem-diameter data from the 13 species of *Moringa* (Moringaceae, Brassicales, Rosids II), which range from massive trees to small shrubs found across dry habitats of mostly tropical Africa, Madagascar, Arabia, and India (fig. 1*E*). Hereafter, we refer to these clades as the *Bursera*, *Commiphora*, *Macrocarpaea*, *Moringa*, and *Pedilanthus* clades (table 1). With the exception of *Macrocarpaea*, sampling is dense with respect to total species numbers of the main clades we sampled within *Bursera*, *Commiphora*, *Moringa*, and *Pedilanthus*.

For *Bursera*, *Commiphora*, and *Pedilanthus*, we followed Olson and Rosell's (2006) protocol for *Moringa* in collecting a small wedge of the outermost wood of adult individuals from the base of the trunk above the roots or any basal swelling beneath the inclined side of the trunk. We collected entire stem segments for stems less than 5 cm in diameter. We measured stem diameter of each individual at the same level where the wood was sampled and calculated an average stem size per species. Carlquist and Grant (2005) used directly comparable methods, making the original data we present here compatible with those previously published for the *Macrocarpaea* and *Moringa* clades. We preserved wood samples in 70% aqueous ethanol and prepared sections using standard histological techniques (Carlquist 1982; Ruzin 1999). We measured 25 randomly selected vessels per sample with a light microscope, measuring a chord intermediate between the maximum and minimum lumen diameter, and averaged values per species.

Phylogenetic Reconstructions

We used phylogenetic hypotheses based on DNA sequence data as a framework for phylogenetic comparative analyses. Phylogenetic reconstructions for *Bursera*, *Commiphora*, and *Macrocarpaea* were newly generated for this study and are described here; taxon accession information and GenBank numbers are listed in table B2. DNA sequence alignments, command files, and trees are available on TreeBase (see "Results"); a summary of the loci and the analyses is provided in table B3. Details of phylogenetic reconstructions for *Moringa* and *Pedilanthus* are reported in Olson (2002) and Cacho et al. (2010).

DNA sequence data for *Bursera* and *Macrocarpaea* were collected for previous publications (see table B3), whereas those for *Commiphora* (cpDNA *psbA-trnH* and *ndhF-rpl32* intergenic spacers, nrDNA external transcribed spacer) were newly gathered following the protocols of Weeks and Simpson (2007) and Shaw et al. (2007). In some cases, modified internal and external primers for the *ndhF-rpl32* intergenic spacer were used (primer sequences available from A. Weeks on request). All data sets were aligned with ClustalW or ClustalX (Larkin et al. 2007) and then verified and adjusted manually. The best-fitting model of sequence evolution for each marker (*Bursera*, *Macrocarpaea*) or the concatenated data set (*Commiphora*) was determined using jModelTest v.0.1.1 (Posada 2008). We rooted analyses of *Bursera* with *Commiphora campestris*, a fellow member of Burseraceae subtribe Burserinae (Thulin et al. 2008), and those of *Commiphora* with *Ambilobea madagascariensis*, a member of Burseraceae tribe Garugeae (Thulin et al. 2008). The *Macrocarpaea* analysis was rooted with Gentianaceae taxa *Symbolanthus macranthus* and *Tachia occidentalis*, per Struwe et al. (2009).

Phylogenetic analysis of *Bursera*, *Commiphora*, and *Macrocarpaea* were conducted using Bayesian inference as implemented by MrBayes v.3.2 (*Bursera*) on the CIPRES portal v.2.2 (Miller et al. 2010) or MrBayes v.3.1.2 (*Commiphora*, *Macrocarpaea*; Huelsenbeck and Ronquist 2001; see table B3). Each analysis was partitioned by marker, except *Commiphora*, and used a random starting tree, with the exception that the heating parameter was lowered to 0.05 in *Bursera* analyses to

improve the probability of exchange between chains. Stationarity was explored using Tracer 1.4 or 1.5 (Rambaut and Drummond 2007, 2009). Following Rambaut and Drummond (2007, 2009), we determined that the trees at stationarity had been drawn from an effectively large population because all estimated parameters had ESS values >100. Posterior probabilities of clades were obtained from the 50% majority-rule consensus tree. Branch lengths were drawn from these topologies (*Bursera*, *Macrocarpaea*) or from that of the maximum clade credibility tree (*Commiphora*) as generated by BEAST's TreeAnnotator program (Drummond et al. 2012).

We built a five-clade supertree to take into account the evolutionary relationships among our five clades simultaneously. To approximate appropriate branch lengths, we assigned ages to nodes by applying results from previous broadscale analyses of estimated divergence times using the "BLADJ" algorithm, as implemented in Phylocomm v4.2 (Webb et al. 2008). We assigned ages to nodes as follows: root, 116.74 million years ago (Mya; node 4 in Magallón and Castillo 2009); most recent common ancestor (MRCA) Moringaceae-Euphorbiaceae-Sapindales, 108.39 Mya (node 5 in Magallón and Castillo 2009); MRCA Moringaceae-Sapindales, 98.43 Mya (node 8 in Magallón and Castillo 2009); *Moringa* crown, 68.77 Mya (Beilstein et al. 2009); MRCA *Bursera-Commiphora*, 54.75 Mya (De-Nova et al. 2012); Gentianaceae, 50.0 Mya (Wikstrom et al. 2001; Yuan et al. 2003); *Bursera* crown, 49.43 Mya (De-Nova et al. 2012); *Macrocarpaea*, 45.0 Mya (Yuan et al. 2003); MRCA *Commiphora lasiodisca–A. madagascariensis*, 32.87 Mya (De-Nova et al. 2012); MRCA *Pedilanthus* clade of *Euphorbia*, 5.0 Mya (Bruyns et al. 2011); and MRCA *Euphorbia finkii–Euphorbia tehuacana*, 3.0 Mya (Bruyns et al. 2011).

Testing the Effect of Phylogeny on Vessel Diameter and on the Vessel Diameter–Stem Diameter Relationship

We tested the effect of membership in the five clades in table 1 on vessel diameter variation and on vessel diameter–stem diameter scaling using a mixed model. This model predicted $\log_{10}$ vessel diameter based on $\log_{10}$ stem diameter and a term reflecting clade membership. We included this "clade" term in the model as a random effect (Raudenbush and Bryk 2002; Goldstein 2003; Zuur et al. 2009). This model allowed clades to have different intercepts; that is, it allowed clades to have different mean vessel diameters for a given stem size. We compared the fit of this model, hereafter model 1, with two additional models. One of these models predicted $\log_{10}$ vessel diameter based on only one term, $\log_{10}$ stem diameter, hereafter model 0, and allowed a single slope and a single intercept for the whole data set. A third model, model 2, was very similar to model 1 but allowed clades to have different vessel diameter–stem diameter scaling exponents in addition to different intercepts. Given that model 0 was nested within model 1, and in turn model 1 was nested within model 2, we could compare model pairs through likelihood ratio tests (LRT) as well as the respective Akaike Information Criterion (AIC) and Bayesian information criterion (BIC). These three models allowed us to test the effects of clade membership on vessel diameter variation and on the vessel diameter–stem diameter relationship. Because each of the five clades represents a cluster of closely related species all sharing a recent common ancestor, it is plausible that the species within clades might resemble one another more closely than the species in other clades. Finding that model 0 best fit the data would mean that clades did not differ in mean vessel diameter for a given stem size or in their vessel diameter–stem diameter scaling. Model 1 fitting the data best would imply that clades differ in mean vessel diameter for a given stem size but not in their vessel diameter–stem diameter scaling. In contrast, finding that model 2 fits best would mean that clades differ in the slopes of their vessel diameter–stem diameter scaling relationships. Analyses were performed in the R statistical environment (R Development Core Team 2009) using the "nlme" (Pinheiro et al. 2012) and "influence.ME" (Nieuwenhuis et al. 2011) packages.

Once we tested whether clade membership explained differences in vessel diameter variation or scaling with stem size, we then explored whether our comparative data showed phylogenetic signal using a molecular phylogeny–based approach. Phylogenetic signal refers to the tendency for closely related species to resemble one another more closely than more distantly related species (Blomberg et al. 2003). We tested for phylogenetic signal in the residuals of linear models predicting $\log_{10}$ vessel diameter based on $\log_{10}$ stem diameter (model 1; Revell 2010). We performed this fitting and testing procedure for each clade, using the individual phylogenetic reconstructions for each clade and the raw branch lengths reflecting molecular substitutions, as well as for all the data pooled, using the supertree with age-assigned nodes. We assessed the phylogenetic signal in the residuals through a randomization procedure based on phylogenetically independent contrasts (Felsenstein 1985) and the K statistic of Blomberg et al. (2003) using the R package "picante" (Kembel et al. 2010). Together with our mixed models (above), our approach should provide a picture of the likely influence of ancestry on variation in the vessel diameter–stem diameter relationship. Finding significant effects of phylogeny under all tests would point to strong differences between clades and a lack of lability in vessel diameter as stem diameter varies. On the contrary, finding little or no significance would suggest marked lability, that is, that vessel diameter varies as a function of stem diameter but not phylogeny.

Testing the Effect of Climate on Vessel Diameter and on the Vessel Diameter–Stem Diameter Relationship

We tested the effect of climate on the vessel diameter–stem diameter relationship by fitting a multiple linear model with climate variables and stem diameter as predictors. We extracted 19 climate variables from WorldClim v.1.4 (Hijmans et al. 2005) for each wood accession (app. A) using the program ArcGIS 9.2 (ESRI 2006) and calculated species averages. Within the 19 environmental variables, those with a similar nature, for example, precipitation or temperature, were strongly correlated with one another. We grouped correlated variables to build four environmental indexes reflecting temperature, precipitation of the wet and warm part of the year, precipitation of the dry and cold part of the year, and temperature seasonality. Variables within each index were correlated with $R \geq 0.68$, except for the variable isothermality within the seasonality index, which was little correlated with all other variables in the climatic data set. We performed a

principal component analysis on each group of variables and used the first principal component of each analysis as climate indexes.

Once the four environmental indexes were calculated for each species, we fitted a multiple model predicting $\log_{10}$ vessel diameter based on $\log_{10}$ stem diameter and using the four environmental indexes as predictors. We tested the significance of all possible interactions between predictors. We identified the influence of climate on the vessel diameter–stem diameter relationship when interaction terms involving $\log_{10}$ stem diameter and a climatic index were significant. If interactions were not significantly different from zero, but the principal effects were, we interpreted climate as contributing to the explanation of vessel diameter variation. We examined whether collinearity between predictor variables was present through the correlation of predictors, variance inflation factors, and the stability of estimated parameters of the model when a variable was removed (Quinn and Keough 2002). We evaluated the relative importance of the variables in the final model using the squared standardized coefficients. A squared standardized coefficient associated with a predictor indicated by how many standard deviations the vessel diameter would change per standard deviation increase in that predictor. We also used the Lindeman, Merenda, and Gold metric, an index that decomposes R^2 and quantifies how much variance is explained by each predictor (Lindeman et al. 1980). Squared standardized coefficients and the Lindeman, Merenda, and Gold metric, therefore, offer two ways of quantifying the relative importance of climate versus stem diameter. We calculated these two measurements of relative importance using the R package "relaimpo" (Groemping 2006).

Results

Sampling and Anatomical Measurements

We provide original data for 182 samples from 51 species in the *Bursera*, *Commiphora*, and *Pedilanthus* clades (tables 1, B1). Data for 32 species in the *Macrocarpaea* and *Moringa* clades were taken from previously published studies (Olson and Carlquist 2001; Carlquist and Grant 2005; Olson and Rosell 2006). Mean vessel diameter ranged from 25 to ~200 μm, and stems varied from 7 mm to 1.2 m in diameter, across a wide range of self-supporting habits and phenologies (table 1).

Phylogenetic Reconstructions

Bayesian analyses of *Bursera*, *Commiphora*, and *Macrocarpaea* sequence data sets resulted in phylogenetic hypotheses with maximal or very high support at most nodes (figs. B1–B3, available online). Details of analyses carried out for this article can be consulted at treeBASE: http://purl.org/phylo/treebase/phylows/study/TB2:S12867 for *Bursera*, http://purl.org/phylo/treebase/phylows/study/TB2:S14247 for *Macrocarpaea*, and http://purl.org/phylo/treebase/phylows/study/TB2:S14241 for *Commiphora*.

Testing the Effect of Phylogeny on Vessel Diameter and the Vessel Diameter–Stem Diameter Relationship

To test the effect of clade membership, we compared the fit of three different models (see "Methods"): one predicting vessel diameter based on stem diameter with a single intercept and a single slope (model 0), one with the additional "clade" random effect allowing a random intercept (model 1), and one with a random intercept as well as a random slope (model 2). Comparisons between models using likelihood ratio tests (LRTs) and the BIC suggested that model 1, with the "clade" term and a random intercept, best fit the data. LRTs indicated that model 1 fit better than model 0 ($LR_{M0-M1} = 17.53$, $P < 0.001$) and model 2 ($LR_{M1-M2} = 4.96$, $P = 0.08$). Likewise, the BIC also pointed to model 1 as having the best fit (model 0 = −180.17, model 1 = −193.31, model 2 = −189.48). Although model 2 had a slightly smaller value of AIC than model 0, these values were very similar (model 0 = −187.36, model 1 = −202.89, model 2 = −203.85). Given that most criteria pointed to model 1 as the best model, we base our interpretation on this model (table 2), including the coefficient (slope) associated with $\log_{10}$ stem diameter as well as the global intercept and the associated coefficients for each clade. That the model with a random intercept (model 1) fit the data better than the one that also included a random slope (model 2) indicated that, while clades differed slightly in mean vessel diameter for a given stem size (fig. 2), vessel diameter–stem diameter scaling was similar between clades. The slope of the vessel diameter–stem diameter relationship was 0.324, with a 95% confidence interval (CI) of 0.285–0.363. The differences between intercepts were very small, with *Commiphora* and *Moringa* having higher and very similar intercepts (and thus slightly wider vessels for their stem diameters), followed very closely by *Macrocarpaea* and then *Pedilanthus* and *Bursera*, clades with identical intercepts (table 2; fig. 2). There was no tendency for the clades from moist habitats (e.g., *Macrocarpaea*) to have higher intercepts for their stem diameters

Table 2

Testing the Effect of Phylogeny on Vessel Diameter and Vessel Diameter–Stem Diameter Scaling

	Linear mixed model	Phylogenetic signal	
		K	P
$\log_{10}$ stem diameter	.324 (.019)	...	...
Intercept	1.508 (.028)	...	...
Bursera	−.034	.25	.73
Commiphora	.049	.17	.62
Macrocarpaea	−.015	.28	.45
Moringa	.034	.18	.13
Pedilanthus	−.034	.50	.59
Five-clade supertree	...	.09	.26

Note. Linear mixed model predicting $\log_{10}$ vessel diameter based on $\log_{10}$ stem diameter (fixed term) and "clade" with a random intercept (model 2; see "Methods"). All terms in model significant with $P < 0.001$. Standard errors in parentheses. Phylogenetic signal per clade and for all data based on the residuals of the regression of $\log_{10}$ vessel diameter on $\log_{10}$ stem diameter. Variable K is Blomberg's et al. (2003) statistic, and P is the significance of a test based on phylogenetically independent contrasts to detect phylogenetic signal.
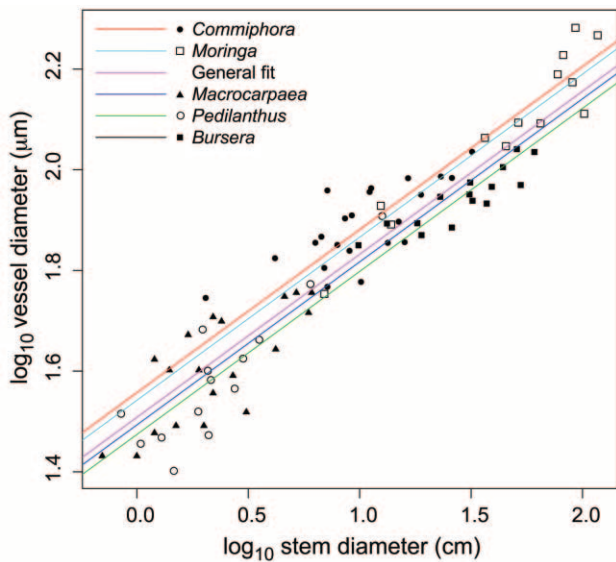
Fig. 2 Scaling of vessel diameter with stem diameter across the means of the 83 species of the five clades studied. The clades have slightly differing y-intercepts, but all have the same scaling exponent (see table 2).

than those from predominantly dry areas (e.g., *Commiphora*; table 2; fig. 2).

Testing the Effect of Climate on the Vessel Diameter–Stem Diameter Relationship and on Vessel Diameter Variation

The species spanned a very wide range of habitats as indicated by environmental variables: mean annual temperature ranged from 9.1° to 28.7°C, mean diurnal temperature fluctuation from 7.9° to 17.7°C, mean annual precipitation from 97 to 3619 mm, and precipitation in the wet quarter of the year from 59 to 1849 mm and in the dry quarter from 0 to 592 mm (table 1). Presumably, this variation should reflect factors of selective importance to plants, for example, water availability. We built four environmental indexes based on the sets of strongly correlated environmental variables (table 3). The mean temperature index was based on six climate variables, whereas the temperature seasonality index and the indexes reflecting precipitation in the wet and dry seasons, respectively, were based on four variables each (table 3). The first principal component, on which each index was based, explained a large percentage, with three of them explaining >88% and that reflecting temperature seasonality explaining 66% (table 3).

The multiple model predicting vessel diameter based on stem diameter and the four climate indexes indicated that the scaling relationship between vessel size and stem size was not affected by climate. We reached this conclusion given the lack of significance of all interaction terms in the model ($P > 0.05$). We then refitted the model with no interaction terms and found that only the terms associated with stem diameter and the temperature index were significantly different from zero (table 4). This model explained 90% of the variation in vessel diameter. Variance inflation factors ranged from 1.25 to 2.06,

suggesting that collinearity between predictors was not strong. The relative importance of the five predictors is reported in table 4 through the squared standardized coefficients and the Lindeman, Merenda, and Gold metric. Both metrics point to stem diameter as the most important predictor in the model. Stem diameter was responsible for 68% of the explained variance in vessel diameter. The temperature index explained just 15% of this variance, whereas all the other indexes explained altogether only 8.4%. Thus, climate did not modify the vessel diameter–stem diameter scaling relationship. Moreover, the temperature index had only a tiny contribution to explaining mean vessel diameter variation (Lindeman, Merenda, and Gold metric = 0.15; table 4). According to the sign of the associated coefficient, larger vessels were positively associated with warmer temperatures in our data set. However, given the amount of variation explained in comparison with stem diameter, the temperature index was only a minor factor associated with differences in vessel diameter.

Discussion

Across the five clades studied, the slope of the vessel diameter–stem diameter scaling relationship was not affected by environment or phylogenetic affinity. Moreover, of all the climate data examined, only temperature seemed to contribute to explaining variation in mean vessel diameter and this very weakly. Here we discuss these results and how they might relate to the general effort to explain the vessel diameter–stem size relationship within and across species. In particular, we discuss our results in the light of recent plant hydraulic models as well as some cautionary notes regarding our sampling and climate variables. However, the pattern of association between vessel diameter and stem diameter (fig. 2) is so marked that it demands explanation regardless of any caveats we present.

We found evidence for marked evolutionary lability of vessel and stem sizes within clades and strikingly similar vessel-stem scaling across clades. We document a consistent pattern of vessel-stem scaling across our data, even though the samples came from five clusters (table 2; fig. 2). Each cluster is a group of closely related species, all descended from the same common ancestor, but these clades are often distantly related. This result implies that the relationship between vessel diameter and stem diameter has the same proportionality across these disparate and distantly related clades. Moreover, we detected only very small differences in y-intercepts between clades. Differences in y-intercept imply larger or smaller vessels for a given stem diameter. For example, based on model 1 (table 2), a stem of 10 cm in diameter in *Commiphora*, the clade with the highest y-intercept, would have an average vessel diameter of just 13 μm greater than *Bursera*, which, as well as *Pedilanthus*, has the smallest y-intercept. Note that this difference is between two clades that come from the same family, Burseraceae, further underscoring the complete lack of any detectable phylogenetic effect. This lack of phylogenetic effect was paralleled by the values of our phylogeny-based tests for phylogenetic structure. Across all of our data, the randomization test (Blomberg et al. 2003) was not significant, and K had very low value (<1), suggesting a lack of phylogenetic signal. The nonsignificant resampling tests and the low K values within clades also showed no tendency for closely related species to resemble one

Table 3

Climate Indexes

Mean temperature	Loadings	Temperature seasonality	Loadings	Precipitation wet	Loadings	Precipitation dry	Loadings
MeanAnnualTemp	.420	MeanDiurnalRange	.337	AnnualPpt	.484	PptDryMonth	.516
MaxTempWarmMonth	.404	TempSeasonality	.558	PptWetMonth	.521	PptSeasonality	−.468
MeanTempWetQtr	.406	TempAnnualRange	.574	PptWetQtr	.524	PptDryQtr	.518
MeanTempDryQtr	.405	Isothermality	−.495	PptWarmQtr	.468	PptColdQtr	.497
MeanTempWarmQtr	.413						
MeanTempColdQtr	.401						
% explained variance	94		66		88		91

Note. Column headings give names of environmental indexes, and associated "Loadings" columns give principal component analysis loadings of the first principal component for each index; the bottommost row gives percent of variance explained by the first principal component. Abbreviations are as follows: Temp, temperature; Max, maximum; WetMonth, wettest month of the year; WetQtr, wettest quarter of the year; DryMonth, driest month of the year; DryQtr, driest quarter of the year; WarmQtr, warmest quarter of the year; ColdQtr, coldest quarter of the year; DiurnalRange, mean daily fluctuation in temperature; Seasonality, coefficient of variation of mean monthly temperature or precipitation; TempAnnualRange, the mean annual fluctuation in maximum and minimum temperatures; Ppt, precipitation.

another more than distantly related ones. As a result, both the linear model with clade membership as a predictor and results based on our molecular phylogenetic reconstructions indicate that phylogenetic affinity does not affect the vessel diameter–stem diameter relationship.

As with clade membership, we found no influence of climate on the slope of the vessel diameter–stem diameter scaling relationship. The only effect of climate detected was the contribution of the temperature index in explaining 15% of the variation in vessel diameter. This effect was very small compared to the percentage of variation explained by stem size (68%). Moreover, this effect of temperature seems difficult to explain given traditional interpretations of the vessel diameter–climate relationship. This result means that there is a very slight tendency for vessels to be wider for a given stem size in areas with warmer temperatures. In general, vessels are thought to be wider in areas with greater moisture availability. However, in the case of our data, higher temperatures are found in more extreme, drier areas ($R = -0.52$ between indexes for temperature and precipitation of the dry period), not the moister ones with more even temperatures, where traditionally wider vessels are expected. It remains to be seen whether a vessel-temperature relationship is a general one, but in any case it is so slight, with an R^2 of just 0.15, that its predictive value is very limited. As a result, we can say confidently that across the five clades studied, climate did not modify the vessel diameter–stem diameter relationship and played a very minor role in explaining vessel diameter variation.

Based on the available climate data, direct adaptation to the environment does not appear to provide an explanation for the variation in mean species vessel diameter across the clades we studied. One possible caveat related to this conclusion is that the lack of environmental association could be the result of resolution limitations of our climate data. For example, in the *Macrocarpaea* clade, many of the samples were collected close to one another geographically (fig. 1, map). These plants may track environmental variation too fine to be reflected by WorldClim's 1 × 1–km resolution or variables such as soils that were not included. Even if this were the case, it is clear that climate has only a very minor role in predicting vessel diameter variation. Traditionally, plants of moist areas are expected to

have wide vessels and plants of dry areas wide ones. In our data, the wet forest *Macrocarpaea* cluster at the lower left of figure 2 with their tiny vessels, whereas samples of dryland *Moringa* reach the upper right with their wide ones, showing that dryland plants can have wider vessels than plants from moist land. That there are dryland plants with wider vessels than some wet forest ones is important but hardly a disputed observation.

Much more significant is our observation that across the clades sampled, plants in moist areas did not have vessels that were wider than their counterparts in dry areas, even when controlling for stem size. Though our sampled clades spanned a range of contrasting environments, all scaled with identical vessel diameter–stem diameter slopes (fig. 2). For example, the *Macrocarpaea* clade species all come from very wet habitats and had the highest annual precipitation (table 1). It might be expected that they would have a higher *y*-intercept than the other clades, denoting wider vessels for a given stem diameter (Carlquist 1989). Instead, the *Macrocarpaea* clade had an intercept above that of *Pedilanthus* and *Bursera*, both of which have representatives in both dry and wet habitats, but below *Commiphora* and *Moringa*, both exclusively dryland clades

Table 4

Multiple Linear Model Predicting $\log_{10}$ Vessel Diameter Based on $\log_{10}$ Stem Diameter and the Four Climate Indexes

	Estimate	betasq	lmg
Intercept	1.508 (.016)***	...	...
$\log_{10}$ stem diameter	.328 (.016)***	.814	.679
Temperature	.014 (.004)**	.023	.147
Seasonality	−.008 (.006)[NS]	.003	.019
Ppt wet period	−.003 (.004)[NS]	.001	.013
Ppt dry period	.006 (.006)[NS]	.003	.052

Note. Interactions between all predictors were tested but not significant (NS) in any case. betasq, squared standardized coefficient; lmg, Lindeman, Merenda, and Gold metric. Ppt, precipitation. Standard errors of parameters in parentheses. Adjusted coefficient of determination $R^2 = 0.90$; ANOVA, $F_{(5,77)} = 154.2$, $P < 0.001$.

** $P < 0.01$.

*** $P < 0.001$.

(table 2). In other words, though the species sampled varied in average vessel diameter from 25 to ~200 μm, this variation was explained largely by stem size. Similarly sized plants had similar average vessel dimensions, whether the plants were growing on a dry Somali plain, in a Mexican tropical forest, or in an Ecuadorian cloud forest. Variables describing precipitation and temperature regimes, traditionally regarded as selective factors acting directly on vessel diameter independently of stem size, therefore seem insufficient to explain the variation in average vessel diameter across the sampled clades (fig. 2).

It might be argued that most of the clades that we sampled include water-storing species and that this characteristic somehow shields the plants from environmental effects. Plants shielded from environmental effects might not show the expected vessel-climate associations. However, the *Macrocarpaea* clade species are not drought resistant, nor are species such as *Euphorbia finkii* in the *Pedilanthus* clade (table 1). Even if all the species were succulent, this fact alone would in no way account for the predictable scaling of vessel diameter with stem diameter observed across clades (fig. 2). Furthermore, direct adaptation to environmental conditions has often been invoked in explaining the xylem anatomical characteristics even in water-storing plants (Olson and Carlquist 2001; Olson 2003). In contrast, our results show quite strikingly that, regardless of environment or anatomical construction, stem diameter predicts vessel diameter across species. As a result, even taking the cautions that we raise into account, the strong pattern of association between vessel diameter and stem diameter stands in need of explanation.

Selection on basipetal vessel widening in the context of stem length-diameter proportions seems a likely component of such an explanation. Our results seem congruent with explanations linking vessel diameter and stem diameter via selection favoring optimal vessel taper in the context of the stem length-diameter relationship. A relation known as the Hagen-Poiseuille law illustrates how increases in conduit length l diminish flow rate Q but that small increases in conduit radius r are sufficient to counteract this drop: $Q = \Delta P/l \cdot \pi r^4/8\mu$, where $\Delta P/l =$ the drop in pressure per unit of conduit length, and $\mu =$ the fluid viscosity (Tyree and Ewers 1991; Zwieniecki et al. 2001; Bettiati et al. 2012). Quantitative models build on the Hagen-Poiseuille law to predict the hydraulic configuration(s) expected to maximize conductivity while minimizing cavitation risk (West et al. 1999; Comstock and Sperry 2000; Mencuccini 2002; McCulloh et al. 2003; Hacke et al. 2006; Sperry et al. 2008; Savage et al. 2010; Hölttä et al. 2011). The link between vessel diameter and stem diameter seems likely via conductive path length. The Hagen-Poiseuille law shows that as total path length increases, flow rate will drop if vessel diameter does not increase. Basipetal widening of vessels can at least partially buffer this drop (Becker and Gribben 2001; James et al. 2003; Zaehle 2005; Fan et al. 2009; Bettiati et al. 2012). The predictable relationship between vessel and stem diameter we recovered across species therefore suggests broadly similar stem length-diameter allometries (Ewers et al. 1990; Sperry et al. 2006). This prediction is borne out by stem length-diameter allometric studies, which document predictable scaling across self-supporting plants (Niklas 1994; Niklas and Spatz 2004; Niklas et al. 2006), and by our observations (table B4; fig. 3). These considerations make it seem likely that
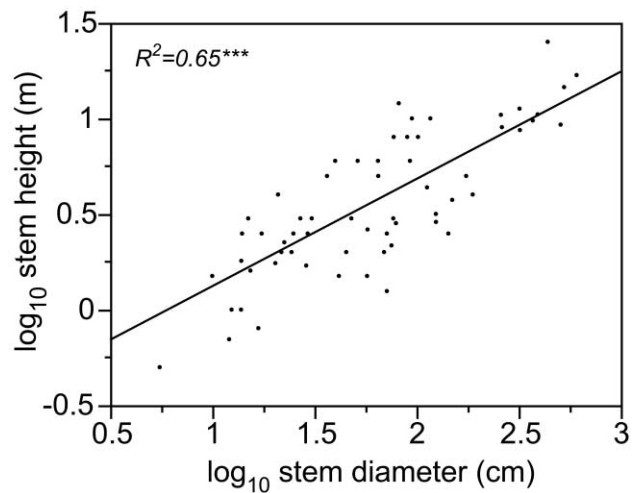

Fig. 3 Stem length-diameter relations across 62 of the studied species to show that predictable patterns of vessel-stem scaling are reflected in predictable patterns of stem length-diameter scaling. Stem length-diameter scaling is expected given vessel-stem diameter scaling (fig. 2) if basal vessel diameter is a function of conductive path length and stem length-diameter proportions are broadly similar across self-supporting plants. Black circles are species means; three asterisks $=$ $P < 0.0001$.

stem diameter and vessel diameter are intimately related through the action of selection via conductive path length. The question then arises as to why the slope of the vessel diameter–stem diameter relationship should be so similar across the sampled clades.

The vessel diameter–stem diameter scaling exponents we recovered here are congruent with a recent scaling model that predicts broadly similar vessel-stem diameter proportionalities across species (Savage et al. 2010; see also West et al. 1999; Enquist 2002, 2003). This model posits as its core notion that many features of organisms reflect the effects of a tug-of-war between selection favoring maximal surface area across which metabolites are assimilated and waste products eliminated and the opposing vector of selection minimizing within-organism transport distances and costs. With dimensionality between two and three, a fractal branching network is as close as possible to a simultaneous maximization of surface area and minimization of transport distance (West et al. 1997). To this basic trade-off, Savage et al. (2010) added a further selective tension, one between the maximization of conductivity via greater basipetal vessel widening and the minimization of cavitation risk, which tends to favor less widening (Ewers and Fisher 1989; Becker et al. 2000; Comstock and Sperry 2000; Cai et al. 2010). Savage et al. (2010) suggest that self-supporting plants should describe a vessel diameter–stem diameter exponent of 0.33 in large data sets. In this model, when vessels widen slowly tip to base (vessel diameter–stem diameter tapering exponents of less than 0.33), it leads to lower-than-optimal conductance (long conductive path length relative to diameter). Tapering exponents above this value lead to slower or even no increase in conductance, depending on plant size, but expose the plants to increasing cavitation risk (Tyree et al. 1994;

Comstock and Sperry 2000; Hacke et al. 2006; Cai and Tyree 2010). Savage et al. (2010) therefore regard 0.33 as a "break-even" point around which the values observed in nature should oscillate. The scaling exponents we recovered (0.324, 95% CI, 0.285–0.363, in the model including "clade"; see table 2; 0.328, 95% CI, 0.297–0.359, in the model including climate indexes; table 4) bracket this value and fall in a similar or slightly higher range as the few previously documented empirical conduit diameter–stem diameter scaling values (including species with tracheids instead of vessels; Ewers and Zimmermann 1984; Enquist 2003; Ewers et al. 2004; Anfodillo et al. 2006; Hacke et al. 2006; Weitz et al. 2006; Coomes et al. 2007; Petit et al. 2008, 2010; Fan et al. 2009; Savage et al. 2010; Petit and Anfodillo 2011). These results seem congruent with the expectation that stem size should be related to vessel diameter via its relationship to conductive path length, with selection favoring taper values providing maximal conduction while simultaneously minimizing cavitation risk.

The explanation of average vessel diameter variation as reflecting optimal taper in the context of conductive path length generates several testable predictions that build on questions raised by our results. For example, vessel diameter changes in ontogeny along the length of stems and even within growth rings (Olson 2007). How such ontogenetic changes parallel or differ from changes in average values across species largely remains to be examined. Hydraulic models predict that vessel taper should reflect conductive path length at any point in the plant. As a result, there is reason to expect similar patterns of vessel-stem diameter relationships both within individuals and across species (Olson and Rosell 2006; Petit et al. 2008, 2010; Bettiati et al. 2012). In any given tree, taper is often most marked in branches, with vessel diameter more constant along the bole, but over large data sets, intraspecific taper patterns should parallel interspecific ones. However, some plants produce vessels that become narrower with age rather than wider (Carlquist and Hoekman 1985), contrary to the increase found here and elsewhere. Our unpublished ontogenetic data show that species such as the succulent *Pedilanthus* have vessels that are wider in the center of the stem than at the periphery. These species produce leafy shoots when actively growing. Once a succulent cane is established, it drops its leaves and persists leafless for several years. Vessel area seems likely to reflect the changing conductive demands in these stems. Such variation in the slopes of within-species ontogenetic trajectories is likely responsible for some of the scatter about the y-intercept observed here. Whatever the slope of a within-species trajectory, however, it is to be expected that vessels should still be proportional to the conductive demands imposed by plant size in tandem with transpirational area. This seems the case here, and even the succulent *Pedilanthus* species, with their wide-to-narrow ontogenetic trajectories, have vessels broadly proportional to their size (fig. 2).

The extent and causes of variation in average vessel diameter in the context of the same stem size also remain to be examined. Anfodillo et al. (2006) suggest that one source of variation is associated with the diameters of vessels at the stem apex. Even given the same vessel diameter–stem diameter scaling slope across species, if some species have wider terminal twig vessel diameters, basal vessels would be expected to be wider for a given distance from the stem apex. Apical vessel diameter likely varies as a function of leaf size and plant habit. Larger leaves are expected to have wider petiole vessels and thus wider vessels at the stem apex. Lianas also seem likely to have wide terminal vessels. In addition, variation in vessel diameter is almost invariably associated with variation in vessel number (Zanne et al. 2010). As a result, it seems likely that some of the variation we observed about the Y-axis should be associated with variation in vessel density (see also Aloni and Zimmermann 1983). In a similar vein, the amount of conductively active xylem seems likely to affect both vessel diameter and density. Species having greater conductively active xylem transectional area would be expected to have narrower vessels. All of these sources of variation, both within and between species, must ultimately be integrated to build an explanation for the patterns of variation in vessel diameter across species, clades, and continents.

Conclusion

It is a common observation that the average vessel diameter of the woody plants growing in a desert will be much narrower than those found in a rain forest. This anatomical pattern appears to be inseparable from the manifestly different average sizes of the plants found in deserts and in rain forests (Moles et al. 2009). Our results, together with similar observations worldwide (Anfodillo et al. 2006; Weitz et al. 2006; Coomes et al. 2007; Mencuccini et al. 2007; Nygren and Pallardy 2008; Sperry et al. 2008; Terrazas et al. 2008; Fan et al. 2009; Petit et al. 2010; Petit and Anfodillo 2011; Olson and Rosell 2013), suggest that selection favoring greater cavitation resistance via narrow vessels will inevitably result in shorter stems and lower-statured plants. Similarly, selection favoring greater stature will inevitably result in wider vessels basally (Gleason et al. 2012). In the absence of selection on vessel diameter via conductive path length, we would expect a wide range of vessel diameter–stem diameter relationships, with dryland species having narrower vessels for a given stem diameter. However, plants with narrow vessels with excessively long stems are likely at a fitness disadvantage relative to those with proportionalities near the point at which the conductive increase conferred by vessel widening is maximal given cavitation risk (Sperry et al. 2006; Savage et al. 2010). Although anatomists have long noted that larger plants have wider vessels and that vessel diameter varies across habitats, they have never provided a quantitative means of taking both considerations into account simultaneously. Our approach integrates stem size explicitly into explanations of vessel diameter variation between individuals across habitats. While much remains to be investigated, results such as those we present here (also Anfodillo et al. 2006; Olson and Rosell 2013) make it seem increasingly plausible that the functional impact of vessel diameter variation cannot be considered as a direct function of water availability but instead only in the context of vessel taper related to stem size.

Acknowledgments

Appendix A

Voucher Information and Localities for Wood Samples

The following information is given for the samples studied in each clade: Latin name, authority, collector and collection number, herbarium where vouchers are deposited, geographic coordinates, locality name, and country.

Bursera clade (Burseraceae): *Ambilobea madagascariensis* (Capuron) Thulin, Beier and Razafim., Weeks 10-I-11–8 GMUF 12°19′13″S, 49°20′14″E, Mt. des Francais, Antsiranana, Madagascar; *A. madagascariensis* (Capuron) Thulin, Beier and Razafim., Weeks 10-I-13–2 GMUF 12°34′49″S, 49°27′30″E, Forêt de Sahafary, Antsiranana, Madagascar; *Bursera arborea* (Rose) L. Riley, Rosell 14 MEXU 19°30′35.73″N, 105°2′12.01″W, Chamela, Jalisco, Mexico; *B. arborea* (Rose) L. Riley, Rosell 15 MEXU 19°30′35.73″N, 105°2′12.01″W, Chamela, Jalisco, Mexico; *B. arborea* (Rose) L. Riley, Rosell 16 MEXU 19°30′35.73″N, 105°2′12.01″W, Chamela, Jalisco, Mexico; *B. arborea* (Rose) L. Riley, Rosell 17 MEXU 19°30′35.73″N, 105°2′12.01″W, Chamela, Jalisco, Mexico; *B. attenuata* (Rose) L. Riley, Rosell 30 MEXU 21°31′10.3″N, 104°58′17.6″W, El Izote, Nayarit, Mexico; *B. attenuata* (Rose) L. Riley, Rosell 32 MEXU 21°31′16.7″N, 104°58′13.35″W, El Izote, Nayarit, Mexico; *B. attenuata* (Rose) L. Riley, Rosell 33 MEXU 21°31′16.7″N, 104°58′13.35″W, El Izote, Nayarit, Mexico; *B. bolivarii* Rzed., Olson 1136113 MEXU 18°0′99″N, 99°32′37.5″W, Xalitla, Guerrero, Mexico; *B. bolivarii* Rzed., Olson 113690 MEXU 18°0′99″N, 99°32′37.5″W, Xalitla, Guerrero, Mexico; *B. bolivarii* Rzed., Olson 113691 MEXU 18°0′99″N, 99°32′37.5″W, Xalitla, Guerrero, Mexico; *B. chemapodicta* Rzed. and E. Ortiz, Olson 1160 MEXU 17°52′14.61″N, 99°34′37.28″W, Cañón del Zopilote, Guerrero, Mexico; *B. chemapodicta* Rzed. and E. Ortiz, Olson 1161 MEXU 17°52′14.61″N, 99°34′37.28″W, Cañón del Zopilote, Guerrero, Mexico; *B. chemapodicta* Rzed. and E. Ortiz, Olson 1162 MEXU 17°52′14.61″N, 99°34′37.28″W, Cañón del Zopilote, Guerrero, Mexico; *B. cinerea* Engl., Rosell 40 MEXU 17°27′22.6″N, 96°48′49.1″W, Jayacatlán, Oaxaca, Mexico; *B. cinerea* Engl., Rosell 41 MEXU 17°26′59.72″N, 96°48′52.77″W, Jayacatlán, Oaxaca, Mexico; *B. cinerea* Engl., Rosell 42 MEXU 17°26′59.73″N, 96°48′52.78″W, Jayacatlán, Oaxaca, Mexico; *B. grandifolia* (Schltdl.) Engl., Rosell 5 MEXU 18°44′14.3″N, 99°11′15.5″W, Atlacholoaya, Morelos, Mexico; *B. grandifolia* (Schltdl.) Engl., Rosell 9 MEXU 18°43′8.1″N, 99°11′9.5″W, Tlaltizapan, Morelos, Mexico; *B. instabilis* McVaugh and Rzed., Rosell 10 MEXU 19°29′53.58″N, 105°2′36.62″W, Chamela, Jalisco, Mexico; *B. instabilis* McVaugh and Rzed., Rosell 11 MEXU 19°29′53.59″N, 105°2′36.63″W, Chamela, Jalisco, Mexico; *B. instabilis* McVaugh and Rzed., Rosell 12 MEXU 19°29′53.6″N, 105°2′36.64″W, Chamela, Jalisco, Mexico; *B. krusei* Rzed., Olson 114140 MEXU 17°7′56.68″N, 99°32′54.54″W, Presa La Venta, Guerrero, Mexico; *B. krusei* Rzed., Olson 114161 MEXU 17°8′11.48″N, 99°32′6.36″W, Presa La Venta, Guerrero, Mexico; *B. krusei* Rzed., Olson 114170 MEXU 17°8′11.48″N, 99°32′6.36″W, Presa La Venta, Guerrero, Mexico; *B. laurihuertae* Rzed. and Calderón, Olson 1168 MEXU 16°20′8.07″N, 95°17′59.25″W, Tehuantepec, Oaxaca, Mexico; *B. laurihuertae* Rzed. and Calderón, Olson 1170 MEXU 16°20′8.07″N, 95°17′59.25″W, Tehuantepec, Oaxaca, Mexico; *B. laurihuertae* Rzed. and Calderón, Olson 1171 MEXU 16°20′8.07″N, 95°17′59.25″W, Tehuantepec, Oaxaca, Mexico; *B. laurihuertae* Rzed. and Calderón, Olson 1172 MEXU 16°20′8.07″N, 95°17′59.25″W, Tehuantepec, Oaxaca, Mexico; *B. longipes* (Rose) Standl., Rosell 6 MEXU 18°0′99″N, 99°32′37.5″W, Xalitla, Guerrero, Mexico; *B. longipes* (Rose) Standl., Rosell 7 MEXU 18°0′99″N, 99°32′37.5″W, Xalitla, Guerrero, Mexico; *B. longipes* (Rose) Standl., Rosell 8 MEXU 18°0′99″N, 99°32′37.5″W, Xalitla, Guerrero, Mexico; *B. ovalifolia* (Schltdl.) Engl., Olson 1095 MEXU 16°25′24.3″N, 92°23′59.4″W, El Puerto, Chiapas, Mexico; *B. ovalifolia* (Schltdl.) Engl., Olson 1096 MEXU 16°25′24.3″N, 92°23′59.4″W, El Puerto, Chiapas, Mexico; *B. ovalifolia* (Schltdl.) Engl., Olson 1098 MEXU 16°8′14.8″N, 92°11′46.2″W, Tzimol, Chiapas, Mexico; *B. ovalifolia* (Schltdl.) Engl., Olson 1099 MEXU 16°8′14.8″N, 92°11′46.2″W, Tzimol, Chiapas, Mexico; *B. ovalifolia* (Schltdl.) Engl., Olson 1100 MEXU 16°8′14.8″N, 92°11′46.2″W, Tzimol, Chiapas, Mexico; *B. ovalifolia* (Schltdl.) Engl., Olson 1128 MEXU 17°9′28″N, 99°35′39.13″W, Puente Papagayo, Guerrero, Mexico; *B. ovalifolia* (Schltdl.) Engl., Olson 1132 MEXU 17°8′18.91″N, 99°32′30.67″W, Puente Omiltepec, Guerrero, Mexico; *B. roseana* Rzed., Calderón and Medina, Rosell 19 MEXU 19°16′23.81″N, 102°4′51.99″W, Cupatitzio, Michoacán, Mexico; *B. roseana* Rzed., Calderón and Medina, Rosell 25 MEXU 19°17′16.2″N, 102°4′30″W, Cupatitzio, Michoacán, Mexico; *B. roseana* Rzed., Calderón and Medina, Rosell 26 MEXU 19°17′16.2″N, 102°4′30″W, Cupatitzio, Michoacán, Mexico; *B. schlechtendalii* Engl., Olson 1156 MEXU 17°52′14.61″N, 99°34′37.28″W, Cañón del Zopilote, Guerrero, Mexico; *B. schlechtendalii* Engl., Olson 1157 MEXU 17°52′14.61″N, 99°34′37.28″W, Cañón del Zopilote, Guerrero, Mexico; *B. schlechtendalii* Engl., Olson 1158 MEXU 17°52′14.61″N, 99°34′37.28″W, Cañón del Zopilote, Guerrero, Mexico; *B. schlechtendalii* Engl., Olson 1190 MEXU 21°12′5.8″N, 89°39′3.4″W, Progreso, Yucatán, Mexico; *B. simaruba* (L.) Sarg., Olson 1145 MEXU 17°3′29.8″N, 99°29′57.36″W, El Zapote, Guerrero, Mexico; *B. simaruba* (L.) Sarg., Olson 1146 MEXU 17°3′29.8″N, 99°29′57.36″W, El Zapote, Guerrero, Mexico; *B. simaruba* (L.) Sarg., Olson 1147 MEXU 17°3′29.8″N, 99°29′57.36″W, El Zapote, Guerrero, Mexico; *B. simaruba* (L.) Sarg., Olson 1148 MEXU 17°3′29.8″N, 99°29′57.36″W, El Zapote, Guerrero, Mexico; *B. simaruba* (L.) Sarg., Olson 1186 MEXU 21°12′5.8″N, 89°39′3.4″W, Progreso, Yucatán, Mexico; *B. simaruba* (L.) Sarg., Olson 1187 MEXU 21°12′5.8″N, 89°39′3.4″W, Progreso, Yucatán, Mexico; *B. simaruba* (L.) Sarg., Olson 1188 MEXU 21°12′5.8″N, 89°39′3.4″W, Progreso, Yucatán, Mexico; *B. simaruba* (L.) Sarg., Olson 1189 MEXU 21°12′5.8″N, 89°39′3.4″W, Progreso,

Yucatán, Mexico; *B. simaruba* (L.) Sarg., Rosell 103 MEXU 19°20′59.81″N, 104°54′8.28″W, Agua Caliente, Jalisco, Mexico; *B. simaruba* (L.) Sarg., Rosell 123 MEXU 19°20′59.81″N, 104°54′8.28″W, Agua Caliente, Jalisco, Mexico; *B. simaruba* (L.) Sarg., Rosell 34 MEXU 19°20′59.81″N, 104°54′8.28″W, Agua Caliente, Jalisco, Mexico; *B. simaruba* (L.) Sarg., Rosell 44 MEXU 18°34′59.12″N, 95°4′34.14″W, Los Tuxtlas, Veracruz, Mexico; *B. simaruba* (L.) Sarg., Rosell 45 MEXU 18°34′59.12″N, 95°4′34.14″W, Los Tuxtlas, Veracruz, Mexico; *B. simaruba* (L.) Sarg., Rosell 46 MEXU 18°34′59.12″N, 95°4′34.14″W, Los Tuxtlas, Veracruz, Mexico; *B. simaruba* (L.) Sarg., Rosell 65 MEXU 19°20′59.81″N, 104°54′8.28″W, Agua Caliente, Jalisco, Mexico; *B. suntui* C. A. Toledo, Olson 1151 MEXU 17°52′38.97″N, 99°34′45.78″W, Cañón del Zopilote, Guerrero, Mexico; *B. suntui* C. A. Toledo, Olson 1152 MEXU 17°52′38.97″N, 99°34′45.78″W, Cañón del Zopilote, Guerrero, Mexico; *B. suntui* C. A. Toledo, Olson 1153 MEXU 17°52′38.97″N, 99°34′45.78″W, Cañón del Zopilote, Guerrero, Mexico; *B. suntui* C. A. Toledo, Olson 1154 MEXU 17°52′38.97″N, 99°34′45.78″W, Cañón del Zopilote, Guerrero, Mexico.

   Commiphora clade (Burseraceae): *Commiphora* "*arafy*" H. Perrier, Weeks 10-II-12–1 GMUF 20°24′23″S, 44°50′32″E, Manaby, Morondava, Madagascar; *C.* "*arafy*" H. Perrier, Weeks 10-II-13–1 GMUF 20°9′54″S, 44°26′44″E, Kirindy, Morondava, Madagascar; *C.* "*arafy*" H. Perrier, Weeks 10-II-13–7 GMUF 20°3′35″S, 44°40′52″E, Kirindy, Morondava, Madagascar; *C.* "*arafy*" H. Perrier, Weeks 10-II-14–7 GMUF 19°51′54″S, 44°36′47″E, Morondava, Madagascar; *C.* "*vezorum*" Capuron, Weeks 10-I-20–9 GMUF 23°19′49″S, 43°55′21″E, Ankiliberengy, Toliara, Madagascar; *C.* "*vezorum*" Capuron, Weeks 10-I-23–8 GMUF 23°31′33″S, 43°45′26″E, Sarodrano, Toliara, Madagascar; *C. ankaranensis* (J.-F. Leroy) Cheek and Rakot., Weeks 10-I-11–13 GMUF 12°19′13″S, 49°20′14″E, Mt. des Francais, Antsiranana, Madagascar; *C. ankaranensis* (J.-F. Leroy) Cheek and Rakot., Weeks 10-I-12–4 GMUF 12°19′59″S, 49°20′56″E, Mt. des Francais, Antsiranana, Madagascar; *C. ankaranensis* (J.-F. Leroy) Cheek and Rakot., Weeks 10-I-12–8 GMUF 12°19′59″S, 49°20′56″E, Mt. des Francais, Antsiranana, Madagascar; *C. ankaranensis* (J.-F. Leroy) Cheek and Rakot., Weeks 10-I-9–5 GMUF 12°14′10″S, 49°21′58″E, Oronjia Peninsula, Antsiranana, Madagascar; *C. aprevalii* (Baill.) Guillaumin, Weeks 10-I-20–4 GMUF 22°57′16″S, 44°20′39″E, Andranovory, Toliara, Madagascar; *C. aprevalii* (Baill.) Guillaumin, Weeks 10-I-20–7 GMUF 22°57′16″S, 44°20′39″E, Ankiliberengy, Toliara, Madagascar; *C. aprevalii* (Baill.) Guillaumin, Weeks 10-I-21–11 GMUF 23°24′41″S, 43°46′48″E, La Table, Toliara, Madagascar; *C. aprevalii* (Baill.) Guillaumin, Weeks 10-I-22–14 GMUF 23°24′41″S, 43°46′48″E, La Table, Toliara, Madagascar; *C. aprevalii* (Baill.) Guillaumin, Weeks 10-I-26–7 GMUF 23°1′28″S, 43°36′59″E, Ranobe, Toliara, Madagascar; *C. aprevalii* (Baill.) Guillaumin, Weeks 10-I-27–1 GMUF 23°2′18″S, 43°41′31″E, Ranobe, Toliara, Madagascar; *C. aprevalii* (Baill.) Guillaumin, Weeks 10-II-13–6 GMUF 20°4′21″S, 44°40′33″E, Kirindy, Morondava, Madagascar; *C. falcata* Capuron, Weeks 10-I-26–3 GMUF 23°1′28″S, 43°36′59″E, Ranobe, Toliara, Madagascar; *C. falcata* Capuron, Weeks 10-I-27–4 GMUF 23°2′18″S, 43°41′31″E, Ranobe, Toliara, Madagascar; *C. franciscana* Capuron, Weeks 10-I-22–10 GMUF 23°24′41″S, 43°46′48″E, La Table, Toliara, Madagascar; *C. franciscana* Capuron, Weeks 10-I-22–8 GMUF 23°24′41″S, 43°46′48″E, La Table, Toliara, Madagascar; *C. grandifolia* Engl., Weeks 10-I-13–1 GMUF 12°34′49″S, 49°27′30″E, Forêt de Sahafary, Antsiranana, Madagascar; *C. grandifolia* Engl., Weeks 10-I-15–5 GMUF 12°34′49″S, 49°27′30″E, Forêt de Sahafary, Antsiranana, Madagascar; *C. grandifolia* Engl., Weeks 10-I-27–2 GMUF 23°2′18″S, 43°41′31″E, Ranobe, Toliara, Madagascar; *C. humbertii* H. Perrier, Weeks 10-I-20–11 GMUF 23°19′49″S, 43°55′21″E, Ankiliberengy, Toliara, Madagascar; *C. humbertii* H. Perrier, Weeks 10-I-20–8 GMUF 23°19′49″S, 43°55′21″E, Ankiliberengy, Toliara, Madagascar; *C. humbertii* H. Perrier, Weeks 10-I-21–4 GMUF 23°24′41″S, 43°46′48″E, La Table, Toliara, Madagascar; *C. humbertii* H. Perrier, Weeks 10-I-22–5 GMUF 23°24′41″S, 43°46′48″E, La Table, Toliara, Madagascar; *C. humbertii* H. Perrier, Weeks 10-I-23–11 GMUF 23°31′33″S, 43°45′26″E, Sarodrano, Toliara, Madagascar; *C. humbertii* H. Perrier, Weeks 10-I-23–9 GMUF 23°31′33″S, 43°45′26″E, Sarodrano, Toliara, Madagascar; *C. lamii* H. Perrier, Weeks 10-I-26–2 GMUF 23°1′28″S, 43°36′59″E, Ranobe, Toliara, Madagascar; *C. lamii* H. Perrier, Weeks 10-I-26–4 GMUF 23°1′28″S, 43°36′59″E, Ranobe, Toliara, Madagascar; *C. lasiodisca* H. Perrier, Weeks 10-I-11–10 GMUF 12°18′53″S, 49°20′18″E, Mt. des Francais, Antsiranana, Madagascar; *C. mafaidoha* H. Perrier, Weeks 10-I-26–1 GMUF 23°1′28″S, 43°36′59″E, Ranobe, Toliara, Madagascar; *C. mafaidoha* H. Perrier, Weeks 10-I-26–6 GMUF 23°1′28″S, 43°36′59″E, Ranobe, Toliara, Madagascar; *C. mafaidoha* H. Perrier, Weeks 10-II-13–2 GMUF 20°9′54″S, 44°26′44″E, Kirindy, Morondava, Madagascar; *C. mahafaliensis* Capuron, Weeks 10-I-21–1 GMUF 23°24′41″S, 43°46′48″E, La Table, Toliara, Madagascar; *C. mahafaliensis* Capuron, Weeks 10-I-21–12 GMUF 23°24′37″S, 43°46′53″E, La Table, Toliara, Madagascar; *C. mahafaliensis* Capuron, Weeks 10-I-21–2 GMUF 23°24′41″S, 43°46′48″E, La Table, Toliara, Madagascar; *C. mahafaliensis* Capuron, Weeks 10-I-22–1 GMUF 23°24′41″S, 43°46′48″E, La Table, Toliara, Madagascar; *C. mahafaliensis* Capuron, Weeks 10-I-22–2 GMUF 23°24′41″S, 43°46′48″E, La Table, Toliara, Madagascar; *C. mahafaliensis* Capuron, Weeks 10-I-28–3 GMUF 23°34′49″S, 43°57′29″E, Onilahy River, Toliara, Madagascar; *C. marchandii* Engl., Weeks 10-I-21–3 GMUF 23°24′41″S, 43°46′48″E, La Table, Toliara, Madagascar; *C. marchandii* Engl., Weeks 10-I-22–6 GMUF 23°24′41″S, 43°46′48″E, La Table, Toliara, Madagascar; *C. monstruosa* (H. Perrier) Capuron, Weeks 10-I-22–3 GMUF 23°24′41″S, 43°46′48″E, La Table, Toliara, Madagascar; *C. orbicularis* Engl., Weeks 10-I-20–10 GMUF 23°19′49″S, 43°55′21″E, Ankiliberengy, Toliara, Madagascar; *C. orbicularis* Engl., Weeks 10-I-22–11 GMUF 23°24′41″S, 43°46′48″E, La Table, Toliara, Madagascar; *C. orbicularis* Engl., Weeks 10-I-22–9 GMUF 23°24′41″S, 43°46′48″E, La Table, Toliara, Madagascar; *C. orbicularis* Engl., Weeks 10-I-22–4 GMUF 23°24′41″S, 43°46′48″E, La Table, Toliara, Madagascar; *C. orbicularis* Engl., Weeks 10-I-23–10 GMUF 23°31′33″S, 43°45′26″E, Sarodrano, Toliara, Madagascar; *C. orbicularis* Engl., Weeks 10-I-26–5 GMUF 23°1′28″S, 43°36′59″E, Ranobe, Toliara, Madagascar; *C. orbicularis* Engl., Weeks 10-II-13–4 GMUF 20°4′21″S, 44°40′33″E, Kirindy, Morondava, Madagascar; *C. pervilleana* Engl., Weeks 10-I-11–1 GMUF 12°19′13″S, 49°20′14″E, Mt. des Francais, Antsiranana, Madagascar; *C. pervilleana* Engl., Weeks 10-I-13–7 GMUF 12°34′49″S, 49°27′30″E, Forêt de Sahafary, Antsiranana, Madagascar; *C. simplicifolia* H. Perrier, Weeks 10-I-20–1 GMUF 22°54′36″S, 44°20′24″E, Andranovory, Toliara, Madagascar; *C. simplicifolia* H. Perrier, Weeks 10-I-20–2 GMUF 22°54′36″S, 44°20′24″E, Andranovory, Toliara, Madagascar; *C. simplicifolia* H. Perrier, Weeks 10-I-20–3 GMUF

22°54′36″S, 44°20′24″E, Andranovory, Toliara, Madagascar; *C. sinuata* H. Perrier, Weeks 10-I-23–1 GMUF 23°29′34″S, 43°45′42″E, Sarodrano, Toliara, Madagascar; *C. sinuata* H. Perrier, Weeks 10-I-23–6 GMUF 23°29′34″S, 43°45′42″E, Sarodrano, Toliara, Madagascar; *C.* sp. nov. Onilahy, Weeks 10-I-28–8 GMUF 23°34′49″S, 43°57′29″E, Onilahy River, Toliara, Madagascar; *C. stellulata* H. Perrier, Weeks 10-I-10–2 GMUF 12°16′23″S, 49°23′18″E, Oronjia Peninsula, Antsiranana, Madagascar; *C. stellulata* H. Perrier, Weeks 10-I-10–3 GMUF 12°16′23″S, 49°23′18″E, Oronjia Peninsula, Antsiranana, Madagascar; *C. stellulata* H. Perrier, Weeks 10-I-11–6 GMUF 12°19′13″S, 49°20′14″E, Mt. des Francais, Antsiranana, Madagascar; *C. stellulata* H. Perrier, Weeks 10-I-13–10 GMUF 12°34′49″S, 49°27′30″E, Forêt de Sahafary, Antsiranana, Madagascar; *C. stellulata* H. Perrier, Weeks 10-I-13–5 GMUF 12°34′49″S, 49°27′30″E, Forêt de Sahafary, Antsiranana, Madagascar; *C. stellulata* H. Perrier, Weeks 10-I-14–2 GMUF 12°34′49″S, 49°27′30″E, Forêt de Sahafary, Antsiranana, Madagascar; *C. stellulata* H. Perrier, Weeks 10-I-9–1 GMUF 12°14′10″S, 49°21′58″E, Oronjia Peninsula, Antsiranana, Madagascar; *C. tetramera* Engl., Weeks 10-I-11–14 GMUF 12°19′13″S, 49°20′14″E, Mt. des Francais, Antsiranana, Madagascar; *C. tetramera* Engl., Weeks 10-I-11–2 GMUF 12°19′13″S, 49°20′14″E, Mt. des Francais, Antsiranana, Madagascar; *C. tetramera* Engl., Weeks 10-I-11–3 GMUF 12°19′13″S, 49°20′14″E, Mt. des Francais, Antsiranana, Madagascar; *C. tetramera* Engl., Weeks 10-I-12–11 GMUF 12°19′59″S, 49°20′56″E, Mt. des Francais, Antsiranana, Madagascar; *C. tetramera* Engl., Weeks 10-I-13–3 GMUF 12°34′49″S, 49°27′30″E, Forêt de Sahafary, Antsiranana, Madagascar; *C. tetramera* Engl., Weeks 10-I-13–6 GMUF 12°34′49″S, 49°27′30″E, Forêt de Sahafary, Antsiranana, Madagascar; *C. tetramera* Engl., Weeks 10-I-14–1 GMUF 12°34′49″S, 49°27′30″E, Forêt de Sahafary, Antsiranana, Madagascar; *C. tetramera* Engl., Weeks 10-I-9–4 GMUF 12°14′10″S, 49°21′58″E, Oronjia Peninsula, Antsiranana, Madagascar; *C. tetramera* Engl., Weeks 10-I-9–6 GMUF 12°14′10″S, 49°21′58″E, Oronjia Peninsula, Antsiranana, Madagascar; *C. tetramera* Engl., Weeks 10-I-9–7 GMUF 12°14′16″S, 49°22′12″E, Oronjia Peninsula, Antsiranana, Madagascar.

Macrocarpaea clade (Gentianaceae tribe Helieae): *Macrocarpaea angelliae* J. R. Grant and L. Struwe, Grant 4289 NY 4°28′S, 79°10′W, Yangana-Valladolid, Loja, Ecuador; *M. apparata* J. R. Grant and L. Struwe, Grant 4002 NY 4°27′59″S, 79°8′44″W, Yangana-Valladolid, Loja, Ecuador; *M. arborescens* Gilg, Grant 4084 NY 4°6′31″S, 78°57′49″W, Yangana-Valladolid, Loja, Ecuador; *M. bubops* J. R. Grant and L. Struwe, Grant 4046 NY 3°59′24″S, 79°5′48″W, P. N. Podocarpus, Zamora-Chinchipe, Ecuador; *M. gattaca* J. R. Grant, Grant 4209 NY 0°3′S, 78°38′W, Pichincha, Ecuador; *M. harlingii* J. S. Pringle, Grant 4048 NY 3°37′48″S, 78°26′50″W, P. N. Podocarpus, Zamora-Chinchipe, Ecuador; *M. jensii* J. R. Grant and L. Struwe, Grant 4047 NY 3°59′24″S, 79°5′48″W, P. N. Podocarpus, Zamora-Chinchipe, Ecuador; *M. lenae* J. R. Grant, Grant 4013 NY 4°6′31″S, 78°57′49″W, P. N. Podocarpus, Zamora-Chinchipe, Ecuador; *M. luna-gentiana* J. R. Grant and L. Struwe, Grant 4027 NY 4°24′1″S, 79°6′42″W, Yangana-Valladolid, Loja, Ecuador; *M. luna-gentiana* J. R. Grant and L. Struwe, Grant 4028 NY 4°24′1″S, 79°6′42″W, Yangana-Valladolid, Loja, Ecuador; *M. micrantha* Gilg, Grant 3966 NY 5°40′425″S, 77°42′731″W, San Martín, Peru; *M. noctiluca* J. R. Grant and L. Struwe, Grant 3994 NY 4°27′59″S, 79°8′44″W, P. N. Podocarpus, Zamora-Chinchipe, Ecuador; *M. pachystyla* Gilg, Schunke V. 5298 NY 9°5′0″S, 76°8′59″W, Cachicoto, Huánuco, Peru; *M. rubra* Malme, Grant 3449 SBBG 25°20′15″S, 48°54′39″S, Curitiba-Joinville, Paraná, Brazil; *M. sodiroana* Gilg, Grant 4210 NY 0°17′25″S, 78°36′51″W, Pichincha, Ecuador; *M. subsessilis* R. E. Weaver and J. R. Grant, Grant 4020 NY 4°23′8″S, 79°9′3″W, Yangana-Valladolid, Loja, Ecuador; *M. wallnoeferi* J. R. Grant, Wolfe 12269A F 9°30′S, 74°47′W, Huánuco, Peru; *M. wurdackii* R. E. Weaver and J. R. Grant, Smith 4793 US 5°45′S, 77°43′W, B. P. Alto Mayo, Rioja, Peru; *Symbolanthus macranthus* (Benth.) Moldenke, Grant 3973 NY 4°25′22″S, 79°9′4″W, Yangana-Valladolid, Loja, Ecuador; *Tachia occidentalis* Maguire and Weaver, Woytokowski USw-15885 Usw 9°55′30.95″S, 76°13′52.19″W, Huánuco, Peru.

Moringa clade (Moringaceae): *Moringa arborea* Verdc., Olson 714 MO 4°3′8″N, 41°0′2″E, Garse, NE Province, Kenya; *M. borziana* Mattei, Olson 678 MO 3°21′49″S, 38°35′34″E, Voi, Coast Province, Kenya; *M. borziana* Mattei, Olson 707 MO 3°6′0″S, 39°24′0″E, Galana River, Coast Province, Kenya; *M. concanensis* Nimmo, Olson 700 MO 10°28′31″N, 77°44′57″E, Palni Hills, Tamil Nadu, India; *M. drouhardii* Jum., Olson 679 MO 24°56′54.06″S, 46°22′10.39″E, Amboasary, Toliara, Madagascar; *M. drouhardii* Jum., Olson 694 MO 23°27′6″S, 43°55′51″E, Ambohimahavelona, Toliara, Madagascar; *M. drouhardii* Jum., Olson 695 MO 23°31′0″S, 43°45′12″E, Sarodrano, Toliara, Madagascar; *M. drouhardii* Jum., Olson 696 MO 23°20′0″S, 43°40′0″E, Toliara town, Toliara, Madagascar; *M. hildebrandtii* Engl., Olson 693 MO 22°15′0″S, 43°37′0″E, Vorehe town, Toliara, Madagascar; *M. longituba* Engl., Olson 704 MO 3°58′11″N, 41°45′0″E, Mandera, NE Province, Kenya; *M. longituba* Engl., Olson 708 MO 2°10′44″N, 40°7′11″E, Wajir, NE Province, Kenya; *M. longituba* Engl., Olson 712 MO 1°44′1″N, 40°15′36″E, Wajir, NE Province, Kenya; *M. oleifera* Lam., Olson s.n. MO 13°10′0″N, 79°49′0″E, Chennai, Tamil Nadu, India; *M. ovalifolia* Dinter and Berger, Olson 718a MO 23°19′53″S, 15°38′57″E, Namib-Naukluft, Namibia; *M. peregrina* (Forssk.) Fiori, Olson 567 MO 22°54′0″N, 57°40′0″E, Wadi Muaydin, Birkat Al-Mawz, Oman; *M. pygmaea* Verdc., Nugent 25 EA 9°33′0″N, 49°19′0″E, Qardho, Somalia/ Puntland; *M. rivae* Chiov., Olson 677 MO 1°46′6″N, 37°33′51″E, Mt. Baio, E Province, Kenya; *M. rivae* Chiov., Olson 701 MO 3°55′26″N, 41°11′37″E, Mandera, NE Province, Kenya; *M. ruspoliana* Engl., Olson 702 MO 3°56′28″N, 41°10′0″E, Yabicho, NE Province, Kenya; *M. ruspoliana* Engl., Olson 703 MO 3°57′31″N, 41°52′36″E, Mandera, NE Province, Kenya; *M. stenopetala* (Baker f.) Cufodontis, Olson 675 MO 0°42′21″N, 36°1′34″E, Lake Baringo, Rift Valley Province, Kenya.

Pedilanthus clade of *Euphorbia* (Euphorbiaceae): *Euphorbia bracteata* Jacq., Olson 1010 MEXU 18°29′39.6″N, 99°29′50.3″W, Tlamacazapa, Guerrero, Mexico; *E. bracteata* Jacq., Olson 1011–1 MEXU 18°29′13.4″N, 99°30′24.4″W, Tlamacazapa, Guerrero, Mexico; *E. bracteata* Jacq., Olson 1011–2 MEXU 18°29′13.4″N, 99°30′24.4″W, Tlamacazapa, Guerrero, Mexico; *E. bracteata* Jacq., Olson 845–1 MEXU 23°12′9″N, 106°12′6.3″W, Villa Unión, Sinaloa, Mexico; *E. calcarata* (Schltdl.) V. W. Steinm., Olson 806–1 MEXU 16°48′8.22″N, 93°10′43.11″W, Tuxtla Gutiérrez, Chiapas, Mexico; *E. calcarata* (Schltdl.) V. W. Steinm., Olson 806–2 MEXU 16°48′8.22″N, 93°10′43.11″W, Tuxtla Gutiérrez, Chiapas, Mexico; *E. calcarata* (Schltdl.) V. W. Steinm., Olson 892 MEXU 19°29′53.2″N, 105°2′40.2″W, Chamela, Jalisco, Mexico; *E. calcarata* (Schltdl.) V. W. Steinm., Olson 896 MEXU

19°3′41.7″N, 103°47′3.3″W, Colima-Tecomán, Colima, Mexico; *E. calcarata* (Schltdl.) V. W. Steinm., Olson 900A MEXU 18°13′26″N, 102°14′53.3″W, Arteaga, Michoacán, Mexico; *E. calcarata* (Schltdl.) V. W. Steinm., Olson 939 MEXU 16°42′28.09″N, 93°31′44.73″W, Microondas Juárez, Chiapas, Mexico; *E. calcarata* (Schltdl.) V. W. Steinm., Olson 943 MEXU 16°49′43.4″N, 93°5′25.1″W, Cañón del Sumidero, Chiapas, Mexico; *E. coalcomanensis* (Croizat) V. W. Steinm., Olson 883–2 MEXU 18°42′39.9″N, 103°18′53.1″W, Coalcomán, Michoacán, Mexico; *E. coalcomanensis* (Croizat) V. W. Steinm., Olson 886 MEXU 18°42′39.9″N, 103°18′53.1″W, Coalcomán, Michoacán, Mexico; *E. colligata* V. W. Steinm., Olson 867 MEXU 20°17′39″N, 104°58′30″W, Desmoronado, Jalisco, Mexico; *E. colligata* V. W. Steinm., Olson 867–2 MEXU 20°17′39″N, 104°58′30″W, Desmoronado, Jalisco, Mexico; *E. conzattii* V. W. Steinm., Olson 971A MEXU 15°52′19.1″N, 96°24′37.3″W, Cerro Espina, Oaxaca, Mexico; *E. conzattii* V. W. Steinm., Olson 971B MEXU 15°52′19.1″N, 96°24′37.3″W, Cerro Espina, Oaxaca, Mexico; *E. cymbifera* (Schltdl.) V. W. Steinm., Olson 979–2 MEXU 18°24′40.8″N, 97°25′52.4″W, Tehuacán Valley, Puebla, Mexico; *E. cyri* V. W. Steinm., Olson 973 MEXU 17°19′37.2″N, 98°3′40.3″W, San Sebastián Tecomaxtlahuaca, Oaxaca, Mexico; *E. diazlunana* (Lomelí and Sahagún) V. W. Steinm., Olson 887 MEXU 20°44′57.77″N, 103°30′42.42″W, CUCBA, Guadalajara, Jalisco; *E. diazlunana* (Lomelí and Sahagún) V. W. Steinm., Olson 888 MEXU 20°44′57.77″N, 103°30′42.42″W, CUCBA, Guadalajara, Jalisco; *E. diazlunana* (Lomelí and Sahagún) V. W. Steinm., Olson 898–1 MEXU 19°36′42.2″N, 103°59′36.2″W, San Pedro Toxín, Jalisco, Mexico; *E. finkii* (Boiss.) V. W. Steinm., Olson 917–1 MEXU 17°56′49.7″N, 96°29′46.7″W, Flor Batavia, Oaxaca, Mexico; *E. finkii* (Boiss.) V. W. Steinm., Olson 917–2 MEXU 17°56′49.7″N, 96°29′46.7″W, Flor Batavia, Oaxaca, Mexico; *E. lomelii* V. W. Steinm., Olson 848–1 MEXU 25°28′18.5″N, 111°28′51.3″W, Cd. Insurgentes, Baja California Sur, Mexico; *E. lomelii* V. W. Steinm., Olson 853 MEXU 27°9′12.2″N, 112°53′2.7″W, San Ignacio, Baja California Sur, Mexico; *E. lomelii* V. W. Steinm., Olson 854–1 MEXU 27°1′24.1″N, 112°59′46.6″W, San Ignacio, Baja California Sur, Mexico; *E. peritropoides* (Millsp.) V. W. Steinm., Olson 840 MEXU 21°12′44.9″N, 105°3′20.7″W, Las Varas, Nayarit, Mexico; *E. peritropoides* (Millsp.) V. W. Steinm., Olson 840–1 MEXU 21°12′44.9″N, 105°3′20.7″W, Las Varas, Nayarit, Mexico; *E. peritropoides* (Millsp.) V. W. Steinm., Olson 841 MEXU 21°13′41.2″N, 104°59′53.3″W, Las Varas, Nayarit, Mexico; *E. peritropoides* (Millsp.) V. W. Steinm., Olson 974–1 MEXU 17°7′54.8″N, 97°52′22.7″W, Putla, Oaxaca, Mexico; *E. peritropoides* (Millsp.) V. W. Steinm., Olson 974–2 MEXU 17°7′54.8″N, 97°52′22.7″W, Putla, Oaxaca, Mexico; *E. peritropoides* (Millsp.) V. W. Steinm., Olson 996 MEXU 17°13′22.7″N, 100°14′10″W, La Siberia, Guerrero, Mexico; *E. personata* (Croizat) V. W. Steinm., Olson 955–1 MEXU 21°12′5.8″N, 89°39′3.4″W, Progreso, Yucatán, Mexico; *E. personata* (Croizat) V. W. Steinm., Olson 955–3 MEXU 21°12′5.8″N, 89°39′3.4″W, Progreso, Yucatán, Mexico; *E. personata* (Croizat) V. W. Steinm., Olson 955–5 MEXU 21°12′5.8″N, 89°39′3.4″W, Progreso, Yucatán, Mexico; *E. tehuacana* (Brandegee) V. W. Steinm., Olson 981A MEXU 18°29′36.3″N, 97°22′40.3″W, Tehuacán, Puebla, Mexico; *E. tithymaloides* L., Olson 945 MEXU 16°33′20.1″N, 92°48′11″W, Villa de Acala, Oaxaca, Mexico; *E. tithymaloides* L., Olson 947 MEXU 16°22′55.8″N, 95°18′36.6″W, Cerro Guiengola, Oaxaca, Mexico.

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